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DAILY LOCOMOTOR ACTIVITY PATTERNS IN THREE SPECIES OF *CUPIENNIUS* (ARANEAE, CTENIDAE): THE MALES ARE THE WANDERING SPIDERS

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ABSTRACT

The daily locomotor activity patterns of spiders of three large species of the genus *Cupiennius* (Ctenidae) were measured in an artificial 12:12 light:dark cycle. Adult males ($N = 10$) and females ($N = 10$) of each species of these nocturnal Central American wandering spiders were compared. On average, males were 3.5 (*C. coccineus* and *C. getazi*) to 12.7 (*C. salei*) times more active than females. Hence, males are the truly wandering spiders. We suggest that this is due to sexually motivated searching behavior of the males. Of the two sympatric species, the males and the females of *C. coccineus* were on average 3.1 times more active than those of *C. getazi*. In addition *C. coccineus* exhibited a relative minimum in its locomotor activity when *C. getazi* showed its absolute maximum. This difference in activity pattern may contribute to the reproductive isolation of these two sympatric species.

INTRODUCTION

In the field adult and subadult wandering spiders of the species *Cupiennius salei* (Keyserling) are quite sedentary. Identified individuals were previously found in their retreats on the same dwelling plants for at least one week (Barth and Seyfarth 1979; Seyfarth 1980). We verified this finding during a recent stay in Central America (Barth, Baurecht, Schmitt, unpubl. data) for *C. salei* and extended its validity to *C. coccineus* F. P.-Cambridge and *C. getazi* Simon. Our general impression, however, was that males of all three species moved around more than the females during their nocturnal activity period.

Vibratory courtship behavior of the males of these three *Cupiennius* species is released by pheromones on the silken threads of females (Rovner and Barth 1981; Barth 1989). Hence, males must find the female silken threads and the females themselves for reproducing. We therefore conjectured that the male might locomote more than the female *Cupiennius*.

C. getazi and *C. coccineus* are sympatric species (Barth et al. 1988). Female pheromones and, more importantly, male vibratory signals contribute to reproductive isolation (Barth 1989). Differences in the daily activity patterns of the two species might be an additional mating barrier between them.

The primary purpose of this study is to delineate the extent to which differences in locomotor activity occur among the sexes and the species. A

valuable byproduct of our measurements are data on the time of day to be chosen for behavioral and physiological experiments.

MATERIAL AND METHODS

Spiders.—All spiders were laboratory bred adult males and females of three large species of Central American nocturnal ctenids: *Cupiennius salei* from Mexico, *C. getazi* and *C. coccineus* from Costa Rica (for general biology and taxonomy see Melchers 1963; Lachmuth et al. 1984; Barth et al. 1988). 20 spiders of each species (10 males and 10 females, all virgins) were used. *C. salei* males were 14.5 ± 1.2 months old (mean ± SE) and weighed 2.43 ± 0.2 g (mean ± SE), females were 14.3 ± 1.3 months old and weighed 3.44 ± 0.2 g. The values for *C. coccineus* were 11.8 ± 0.2 months and 1.73 ± 0.1 g for the males and 11.8 ± 0.4 months and 2.92 ± 0.2 g for the females. For *C. getazi*, the corresponding values were 12.5 ± 0.3 months and 0.94 ± 0.1 g for the males and 12.6 ± 0.2 months and 1.5 ± 0.1 g for the females.

Activity measurements.—The activity of each individual spider was measured continuously for 72 hours using an actograph (Animex, Farad type DSEP), the activity registered during one 10 min period being considered as one data point. The actograph was installed in a light-proof room with a 12:12 L:D cycle and a temperature of 25 ± 1°C. These light and temperature conditions are similar to those prevailing in the natural habitat of *Cupiennius* (Barth et al. 1988). All noisy parts of the Animex system were kept outside the experimental room. During the photophase the room was illuminated with fluorescent tubes (Neon-Freon type). The spiders were transferred within their glass jars into this room at least three days before their activity was actually monitored. This time period suffices to entrain *Cupiennius* by an artificial 12:12 L:D cycle (Seyfarth 1980). All spiders were fed four muscid flies once a week on the same day.

During the 72 hours of measurement, the spiders were kept individually in transparent plastic cages (27×20×5 cm). We used one cage for males and another one for females. Between trials, the cages were cleaned. Water was supplied in the cages. During a trial the ceiling of the cage was covered with a wet cloth netting to keep the relative air humidity at >95% inside the cage, a value often found in the natural habitat of the spiders (Barth et al. 1988). No retreat was provided for the spiders. The cage was shielded from direct illumination of the room and illuminated from outside and 1m above by a 60W bulb (Wolfram thread, frosted glass, 2800°K) during the light-on phase. The light intensity inside the cage was 300 Lux. No unusual behavior of the spiders was observed after the three days of encagement.

Calibration.—The Animex system detects the motion of the spider by measuring the disturbance of a magnetic field. Leg movements alone are not detected. The influence of body weight and speed of locomotion of the encaged spider on the measurements was evaluated by the following experiments:

(*a*) The mean speed during bouts of spontaneous locomotion of males and females, regardless of species varies between 5 and 89 mm/s, averaging 30 mm/s (SD ± 16 mm/s; $N = 6$, $n = 60$). A narcotized spider was moved on a piece of cardboard by an electrically driven device over a constant distance through the magnetic field of the Animex system at two speeds, of which the first was close to

the above mentioned average (36 mm/s) whereas the second was higher by almost 200% (106 mm/s). This large increase in speed increased the number of impulses registered by only 5%. Thus, this experiment demonstrated that the speed of locomotion of the encaged spider had virtually no influence on the measurements.

(*b*) Spiders weighing 1 g and 4 g respectively, were moved at the same speed (36 mm/s) through the magnetic field. A spider had to be moved between 26 mm (if 4 g) and 32 mm (if 1 g) to elicit one impulse in the Animex system. Thus, an increase in body weight by 300% increased the number of impulses registered by roughly 23%. We corrected all the data for body weight. Body weight of each spider remined nearly constant during the three days of measurements (weight losses amounted to ca. 3% within one week without food).

The number of impulses registered by the Animex system was tranformed into distance (meters) covered by the spider, using the above data.

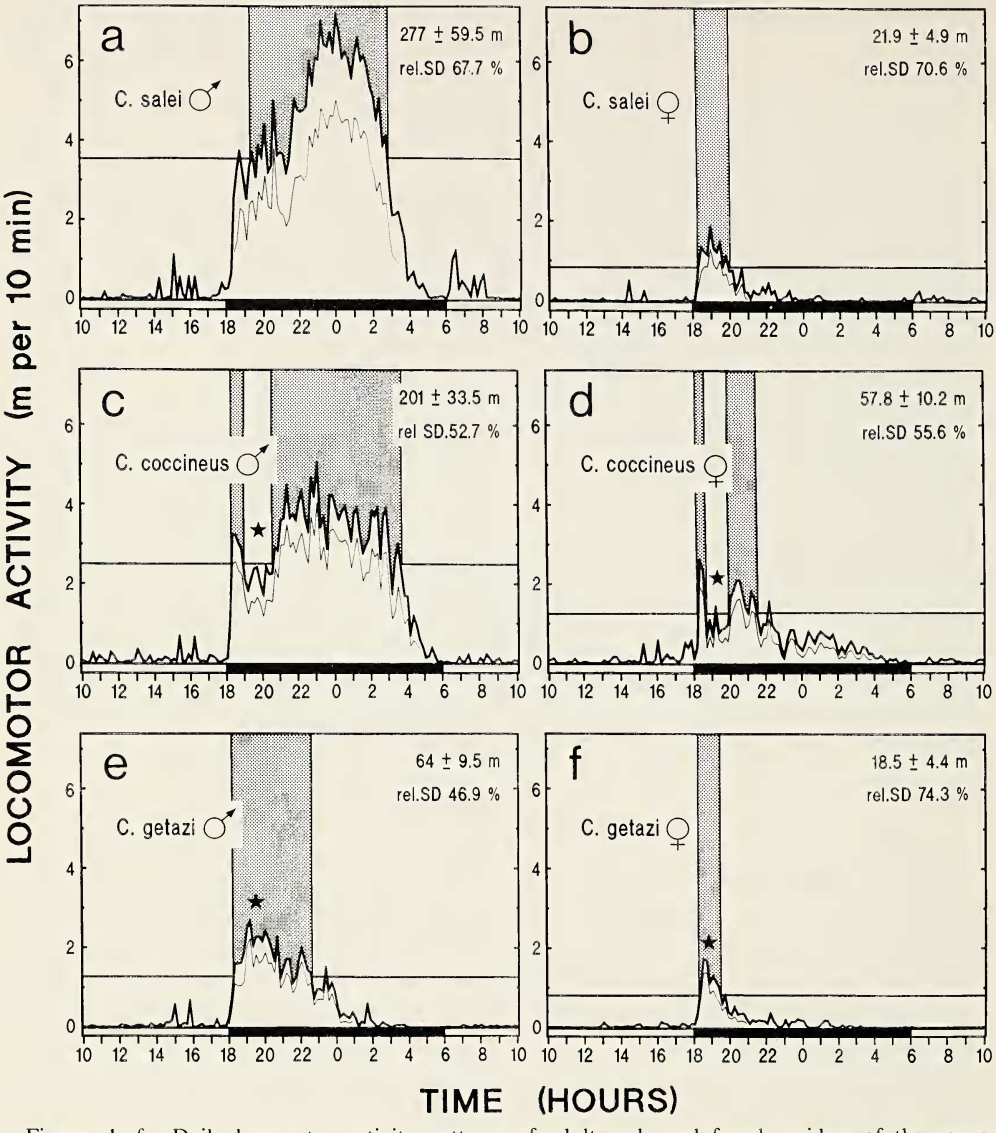
Evaluation of data.—We calculated the total daily amount of activity [given in meters, mean ± SE and % rel. SD = (SD/mean) × 100] and determined the duration of the daily activity period and of the period of maximum activity. Periods of maximum activity (dotted areas in Fig. 1) were defined as times of scotophase during which activity of a spider exceeded 50% of the highest value found. All individual data were compared to the mean. They were considered to follow the mean pattern if their period of maximum activity had roughly the same duration (± 25%) as the mean and was not shifted by more than 50% of that duration to the left or right on the time axis. Peaks and minima of activity were ignored in this context if they lasted for only 10 min.

RESULTS

The results of the measurements of daily activity patterns of groups of 10 spiders separated by species and sex are presented in Fig. 1. All 20 *C. getazi*, 18 of 20 *C. salei* and 13 of 20 *C. coccineus* showed individual activity patterns very similar to the mean. The interindividual variability in the total amount of activity is large: The rel. SD are between 47% (*C. getazi* males) and 74% (*C. getazi* females, see Fig. 1, insets).

The following comments refer to the mean values. Deviations from them by individual spiders are indicated where necessary.

General features of activity periods.—The data clearly confirm that all three species of *Cupiennius* are nocturnal. Only 4.1% of the total daily activity of the males (average of all species) and 8.7% of that of the females (average of all species) was in the light phase. Activity begins immediately after the lights were extinguished and within 20 min after the onset of darkness, all spiders showed activity values larger than 50% of the absolute maximum values (Fig. 1, 1800-1820). Thus light-off is a very effective Zeitgeber which promptly activates the spiders. Periods of maximum locomotor activity lasted about three times longer in males than in females (in five females of *C. coccineus* the period of maximum activity lasted longer than the average, up to 0200). In both males and females the absolute activity maxima occurred long before the end of the dark phase. The decline was more abrupt in the male *C. salei* and *C. coccineus* than in females of all three species and in the males of *C. getazi*.



Figures 1a-f.—Daily locomotor activity patterns of adult male and female spiders of the genus *Cupiennius* (in all cases $N = 10$); mean (thick line) and standard error (thin line; only lower limits are shown). The total amount of activity (m) is given by the numbers in the right upper corner (mean, standard error and relative SD). Horizontal lines indicate 50% of maximum activity. Shaded areas represent time periods of maximum activity. Star marks time of maximum activity in *C. getazi* and of relative minimum in *C. coccineus*. Black area on time axis indicates dark period (1800 to 0600).

Interestingly, both male and female *C. coccineus* became relatively inactive at the same time during the dark phase, i.e. between about 1900 and 2000 (see star in Fig. 1c,d). After 1-2 h they resumed activity to almost the same degree as at the onset of the scotophase.

The time course of the activity of adult *C. salei* females in our present experiments was similar to that previously reported by Seyfarth (1980) for subadult females of the same species. As is known from Seyfarth's (1980) experiments, this activity pattern reflects a biorhythm.

Differences between the sexes.—The average total amount of locomotor activity of males was 3.5 (*C. coccineus* and *C. getazi*) and 12.7 (*C. salei*) times larger than that of females (Fig. 1). Periods of female maximum activity fell within the periods of maximum male activity (Fig. 1). However, the males of *C. getazi* continued to move around at a high rate for about 4 hours and those of *C. salei* and *C. coccineus* for about 7 hours after the end of the period of female maximum activity (Fig. 1).

The following deviations of individuals of *C. coccineus* from the mean *C. coccineus* activity patterns were observed. Three of the *females* exhibited 5 to 8 activity maxima with zero activity in between instead of a relative minimum at the usual time between about 1900 and 2000. The four exceptional *males*, on the other hand, had their locomotor activity evenly distributed between about 1800 and 0400.

Differences between sympatric species.—The activity periods of the two sympatric species, *C. coccineus* and *C. getazi*, partly overlap, i.e., there was no allochrony (Fig. 1c-f). Apart from the fact that *C. coccineus* males and females were on average 3.1 times more active than *C. getazi* males and females, three remarkable features of the activity patterns of these two species emerge.

(*i*) *C. getazi* males and females had their absolute activity maxima between 1830 and 2230 and between 1830 and 1930, respectively (star in Fig. 1e,f). During the same time period, *C. coccineus* males (1900 to 2030) and females (1830 to 2000) exhibit a relative minimum in their activity patterns (star in Fig. 1c,d). Absolute activity values of both species were similar during that time period (for exceptions see preceding section).

(*ii*) The activity of *C. coccineus* males is distributed over nearly the whole dark phase of 12 hours (but see relative minimum, above), whereas *C. getazi* males are only active during the first 8 hours of the dark phase. Correspondingly, the female activities last longer in *C. coccineus* (from about 1800 to 0200, but see minimum, above) than in *C. getazi* (about 1800 to 0200).

(*iii*) *C. coccineus* spiders were most active when the activity of *C. getazi* was already decreasing (Fig. 1c-f).

DISCUSSION

Thre are several studies on biorhythms of spiders which have been the subject of a recent review by Cloudsley-Thompson (1987). To our knowledge, however, so far no data are in the literature on sex-related differences in the amount of locomotor activity. Likewise, no comparative data on the activity patterns of closely related spider species are available.

Differences between the sexes.—Field observations on population structure and laboratory studies on courtship behavior of *Cupiennius* (Rovner and Barth 1981; Barth 1989) suggest that sexually motivated searching behavior is the main factor causing the differences in amount of locomotor activity between males and females. Antipredatory behavior and search for prey or a retreat might be additional or alternative factors influencing locomotor activity. The following arguments are considered as evidence against their importance in the given context.

(*i*) *Predators*: The spiders were not exposed to predators nor disturbed by any obvious stimuli from outside during the measurements. Even if unnoticed stimuli would have been present, they should have influenced males and females in a similar way and therefore cannot account for the observed differences between the sexes.

(*ii*) *Search for prey*: All spiders were fed according to the same regime with no feeding during the time of measurements. *Cupiennius* is a sit-and-wait predator (Melchers 1963; Barth and Seyfarth 1979). The spiders of all three species come out of the retreat at dusk as first described by Barth and Seyfarth (1979), and, as a rule, move less than one meter on their dwelling plant (pers. obs. Barth, Baurecht, Schmitt). There are no known differences in predatory behavior between males and females. There is no indication that the search for prey could account for the differences in locomotor activity between the sexes.

(*iii*) *Retreats*: Retreats of the females are often found to be partly or completely closed by compact web sheets. This is never observed for males, neither in the laboratory nor in the field. Females build their egg sacs and take care of them for about three weeks while in their retreats. Spiderlings often hatch within the retreat and live there for about one week before they disperse. We assume that retreats are more important for females and that they might therefore search more intensively for adequate retreats than males when held in barren cages. Despite the complete absence of retreats in the cages, the males were the much more active sex.

Differences between sympatric species.—The number of interspecific encounters in sympatric species is not only determined by their spatial proximity or distance and by their absolute amount of activity, but also by the degree of temporal overlap of their activity periods.

Our data suggest that activity patterns may indeed contribute to reproductive isolation of the two sympatric species, *C. coccineus* and *C. getazi*. The probability of encountering each other is reduced because (i) *C. coccineus* has a relative minimum during the time period of the absolute activity maximum of *C. getazi* and (ii) *C. coccineus* is most active when the activity of *C. getazi* is already decreasing.

The few individual deviations from mean activity patterns do not weaken the above conclusions since temporal isolation has to be considered as a parameter describing two or more groups of individuals (populations) and not single individuals. Thus, mean (population) patterns have to be compared.

Differences in the amount of activity among the three species.—Interspecific differences in total amounts of activity are hard to interpret with the limited knowledge at hand. They could reflect differences in population density, the males of the species with greater population density being less active because of higher chances for finding a female. Data from our field work show, however, that, given similarly high dwelling plant densities, population densities of the three *Cupiennius* species are similar (Barth, Baurecht, Schmitt in prep.).

The rather high absolute values of total amount of activity found in our experiments should not simply be transferred to the primary forest situation. We instead suggest that the activity was particularly high in our cage situation because of the unattractive environment with no retreat, no prey, no sexual partner and no dwelling plant.

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